

widening out cannot be commenced far up, appears to lie between the utmost improvement of the channel at the expense of accretion on the foreshores outside, and the maintenance of the depths over the foreshores beyond the outlet accompanied with a somewhat less good channel in the estuary. In some cases, deposit on the foreshores at the side beyond the outlet might be of no importance, and then the river channel should be primarily considered ; but if, on the contrary, accretion on the foreshores outside is undesirable, the outlet must be maintained by a greater widening out of the training walls. The actual direction of the training walls must be determined, in each case, by the general direction of the channel above, the situation of ports on the estuary, the position of the outlet, and the set of the flood tide at the entrance.

*Concluding Remarks.*—In terminating this record of my investigations, and the general principles for training works which they seem to indicate, I desire to acknowledge the care with which my assistant, Mr. E. Blundell, has carried out the tedious task of working the tides in the model, and prepared the charts of the experimental results from which the illustrations accompanying this paper have been drawn out. Eddies at sharp edges, due to distortion of scale, appear to have excessive scouring effect in a model ; whilst the action of the more regular currents exhibits a deficiency in scouring power, as previously noted. Though the actual depths of the channels, however, are too small for the distorted vertical scale, reliance, I think, may be placed on the general forms and relative depths of the channels obtained in a model. It is possible that the inadequate depth might be remedied by the employment of a finer or lighter material for forming the bed of the model, or by using a liquid of greater density than water ; but sand and water have the unquestionable advantage of being the substances which actually effect the changes in estuaries.

“On the Cranial Nerves of Elasmobranch Fishes. Preliminary Communication.” By J. C. EWART, M.D., Regius Professor of Natural History, University of Edinburgh. Communicated by Professor BURDON SANDERSON, F.R.S. Received February 22,—Read March 7, 1889.

Although the cranial nerves of *Hexanchus*, *Echinorhinus*, and *Scyllium* have been fully described, and the segmental value of the nerves of Elasmobranch fishes repeatedly considered, the nervous system of *Læmargus* has hitherto escaped notice. This is probably to be accounted for by anatomists taking for granted that *Læmargus* agreed in the arrangement of its nerves with *Echinorhinus* and other *Spinacidae*.

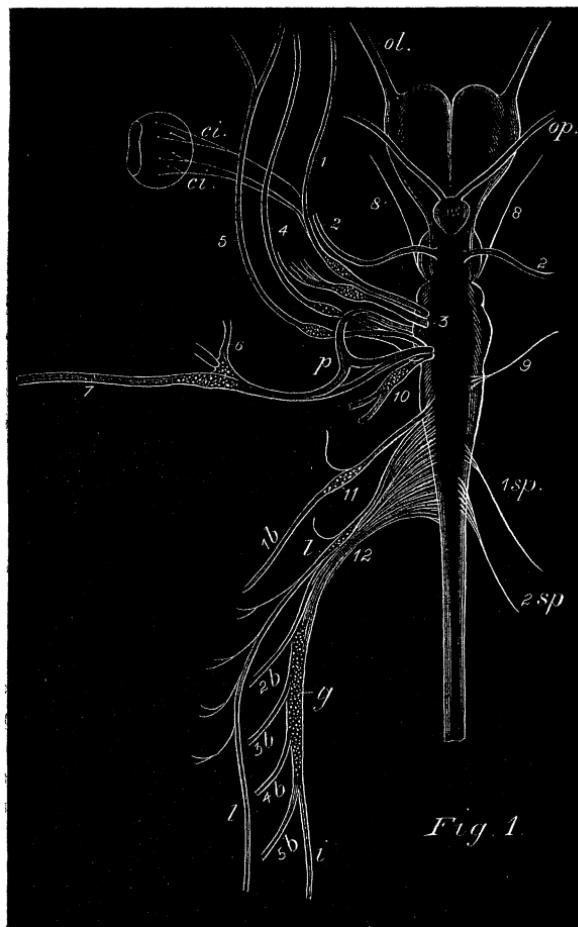
I have not yet had an opportunity of comparing *Læmargus* with either *Hexanchus* or *Echinorhinus*, but I have satisfied myself that the accounts given of the cranial nerves of these forms are not applicable in several important respects to the cranial nerves of *Læmargus*, nor yet to the nerves of the common skate (*Raia batis*). Further, I find that when, having mastered the arrangement of the cranial nerves of *Læmargus* and *Raia*, one turns to *Petromyzon*, *Scyllium*, *Galeus*, and other familiar forms, it is impossible to accept many of the statements hitherto made as to the nature, distribution, and segmental value of the cranial nerves of vertebrates.

In this preliminary communication I propose to describe shortly the cranial nerves of *Læmargus* and *Raia*, reserving for a future paper a comparison between the nerves of *Læmargus* and other Elasmobranchs, and the consideration of the segmental value and the more important modifications of the cranial nerves in the chief subdivisions of the vertebrate group.

### I. The Cranial Nerves of *Læmargus*.

As the olfactory and optic nerves closely resemble those of *Hexanchus*, it is unnecessary to refer to them in this preliminary note, and instead of beginning, as is usually done, with the oculo-motor, I shall first describe the ophthalmicus profundus.

1. *The Ophthalmicus Profundus*.—This nerve has usually been said to belong either to the oculo-motor or to the trigeminal. It presents a root, more or less distinct, a root ganglion, and a trunk which gives off a number of well-marked branches. Although the segmental value of the ophthalmicus profundus need not now be discussed, it may be mentioned that since van Wijhe demonstrated that it possessed a ganglion, its right to rank as a separate cranial nerve has been deemed worthy of consideration. Although Marshall and Spencer concluded that there was nothing in support of the view that the root of this nerve belonged to the trigeminal, and believed that its trunk was a branch of the oculo-motor, Gegenbaur has recently stated that he considers the ophthalmicus profundus with its ganglion as part of the trigeminal. Very different views have been held as to the ganglion of the ophthalmicus profundus. By Marshall and Spencer the ganglion was said to belong to the oculo-motor, and was identified as the ciliary ganglion. Beard, on the other hand, considers the ganglion of the ophthalmicus profundus as homologous with the Gasserian ganglion, while he thinks the ciliary ganglion probably corresponds to a sympathetic ganglion. Believing, with van Wijhe, in the possible existence of two ganglia, one on the ophthalmicus profundus and one (the ciliary) in connexion with the oculo-motor, Beard has given to the ganglion of the ophthalmicus



profundus the name of meso-cephalic. He further states that there can be no doubt that the ciliary (as distinguished from the mesocephalic) ganglion of lower vertebrates is exactly homologous with the ciliary ganglion of mammals.

The ophthalmicus profundus nerve (1, fig. 1) in *Læmargus* arises by several rootlets (2—5) from the side of the medulla immediately in front of the main root of the trigeminal, and runs outwards in contact with the anterior surface of the trigeminal to enter the large foramen which serves for the passage of the trigeminal, and the anterior portions of what may best be known as the facial complex. As the ophthalmicus approaches the foramen it partly blends with the trigeminal, and while in the foramen it communicates with this nerve by

several small branches. On escaping from the cranial wall the ophthalmicus profundus separates from the trigeminal and presents a slight swelling, the meso-cephalic ganglion (Beard), or ciliary ganglion (Gegenbaur and others). This ganglion lies dorsal to, but only very slightly in front of, the large Gasserian ganglion of the trigeminal (3, fig. 1). From the ganglion the trunk extends forwards over the external rectus muscle to pass under the rectus superior towards the eyeball, from which it bends inwards between the superior oblique and internal rectus muscles, to reach the snout by penetrating the pre-orbital process of the cranium.

The more important branches of the ophthalmicus profundus are (1), a small branch which passes outwards above the superior rectus muscle; (2), two or three ciliary branches (*ci.*, fig. 1), which run forwards under cover of the rectus superior to enter the eyeball—to these ciliary branches delicate filaments pass from the deep branch of the oculo-motor; (3), small branches which pass outwards in front of the eyeball; (4), branches to the skin, and subcutaneous tissue of the snout and to the rostral cartilage. I have been unable to trace any branches from the ophthalmicus profundus to either the mucous canals or the ampullæ of the sensory tubes: long and slender branches, however, seem to be distributed to the tubes which extend from the ampullæ to open through the skin.

2. *The Oculo-motor Nerve.*—Although this nerve does not necessarily stand in the same relation to the ophthalmicus profundus as does the ventral root to the dorsal root of a spinal nerve, it will be convenient to deal with it before considering the trigeminal. The oculo-motor has been ranked very differently by different observers. Marshall and Spencer considered it of segmental value, and Gaskell has recently stated that it retains in its root vestiges of a ganglion. Van Wijhe looks upon the oculo-motor as forming the ventral (motor) root of the ophthalmicus profundus, whilst Gegenbaur neither admits that it has the rank of a segmental nerve nor feels satisfied that it represents the ventral root of the ophthalmicus profundus.

The oculo-motor (2, fig. 1) in *Lamargus* arises by a number of delicate rootlets (5—7) from the under-surface of the mid-brain, on a level with the posterior end of the optic lobes and in line with the abducens and spinal nerves. Passing outwards it escapes from the cranial cavity by a special foramen, and bends round the orbital process of the palato-pterygoid arch to reach the rectus superior, where it divides into a superficial and a deep branch. The superficial supplies the superior and internal recti muscles, the deep branch passing under the rectus superior sends filaments to the inferior rectus and inferior oblique muscles, and, as it runs over the pedicle, it sends one or two exceedingly delicate twigs to the ciliary branches of the ophthalmicus profundus. I have been unable to find any

ganglionic cells that might represent a root ganglion in any part of the oculo-motor nerve or any representative of a ciliary ganglion, in addition to the ganglion of the ophthalmicus profundus, or even any communication between the oculo-motor nerve and the ganglion of the ophthalmicus profundus, which has apparently been often described as the ganglion of the oculo-motor nerve, *i.e.*, as the ciliary ganglion.

3. *The Trigeminal Nerve.*—Hitherto anatomists have, with few exceptions, described the trigeminal nerve as arising in Elasmobranchs by several roots, but there has seldom been complete agreement as to either the number or position of the roots, and hence great confusion has arisen. Marshall and Spencer did much to remove this confusion by showing that the so-called dorsal root of the trigeminal undoubtedly belonged to the facial. They described the trigeminal as arising by a small anterior non-ganglionic root and a large posterior ganglionic root. Their small anterior root evidently corresponds to the root of the ophthalmicus profundus, the ganglion of which they transferred to the oculo-motor.

In *Laemargus* the origin of the trigeminal (3, fig. 1) is easily made out. When the rootlets of the ophthalmicus profundus are removed, the trigeminal is found to spring from the side of the medulla by a single large root (the posterior root of Marshall and Spencer), which lies in a line with the ventral roots of the facial complex. The root of the trigeminal passes forwards and, blending with the ophthalmicus profundus, enters the foramen under cover of two of the subdivisions of the facial complex, viz., the ophthalmicus superficialis and buccal. As it passes through the foramen it presents a distinct swelling—the Gasserian ganglion. The trunk of the nerve at once divides into two large branches—the maxillary and mandibular. A third but slender branch (the superficial ophthalmic branch of the trigeminal) springs either from the trunk or from the mandibular. Two very slender nerves, which leave the root as it crosses the cranial cavity, pass upwards through the walls of the cranium towards the skin in front of the ear capsule.

The branches of the trigeminal are : (1) the superficial ophthalmic which runs first along the inner and then obliquely over the upper surface of the ophthalmicus superficialis of the facial complex, to pass through a special canal in the pre-orbital cartilage and send branches to the subcutaneous tissue of the snout, especially in front of the preorbital process. (2) The maxillary branch. This nerve runs forwards and outwards under the eye muscles, dividing on the way into branches, which reach the under surface of the snout and terminate in the vicinity of the anterior labial and palato-pterygoid cartilages. The trunk and its various branches are intimately related to the buccal subdivision of the facial complex. (3) The

mandibular branch. This large nerve first gives off a number of small twigs which pass under the buccal division of the facial to assist in supplying the muscles in front of the spiracle. It then divides into branches which pass forwards and outwards supplying the mandibular and other muscles, and finally sends branches to the skin in the vicinity of the mandibular arch and the posterior labial cartilage. Some fibres from both the maxillary and mandibular nerves penetrate between the sensory tubes, and lie in close contact with the mucous canals, but in no case have I found them terminating in the ampullæ or penetrating the mucous canals to end in the sensory tissue lodged in their cavities.

*The Facial Complex.*—In describing the cranial nerves of *Hexanchus*, Gegenbaur considered the trigeminal and facial nerves as forming a single group, and he included amongst the roots of the trigeminal the roots of two nerves (*ophthalmicus superficialis* and *buccal*) now all but universally acknowledged as belonging to the facial.

While in the higher vertebrate the trigeminal nerve is of far more importance than the facial, in the lower fishes it is otherwise; for while the trigeminal proper consists of but a single root the so-called facial is made up of three large roots, one of which seems to be double. Hence, instead of grouping the trigeminal and facial nerves together, it will be more convenient to consider the facial nerves by themselves and speak of them as the facial complex. This complex includes four separate nerves, viz., (1) the *ophthalmicus superficialis*, (2) the *buccal*, (3) the *palatine*, and (4) the *hyomandibular*. In the meantime it is only necessary to mention that the enormous development of the so-called facial is owing to the presence of a complex system of lateral sense organs—sensory tubes and mucous canals.

4. *The Ophthalmicus Superficialis.*—This nerve (4, fig. 1) arises by a large root from the so-called trigeminal nucleus which occupies the most dorsal portion of the medulla. The root, in a large fish, lies on a higher level (by about 4 mm.) than the other roots of the facial complex, and it is also the most posterior root, *i.e.*, the furthest from the snout. Arising far apart from the other divisions of the facial it runs forwards and then bends downwards to reach the buccal nerve, with which it freely communicates as it passes through the cranial walls at a higher level than the trigeminal and *ophthalmicus profundus*. Immediately beyond the walls of the cranium it presents a ganglionic swelling, which consists of large bipolar cells, similar to those of the Gasserian ganglion. The main trunk of the nerve then arches round the conical orbital process of the palato-pterygoid arch, and extends forwards above the eye muscles to send branches to the sensory tubes and mucous canals of the snout.

In *Loemargus* the *ophthalmicus superficialis* of the facial supplies (1) the ampullæ of the sensory tubes on the dorsal aspect of the snout,

and (2) the cranial, rostral, subrostral, and nasal mucous canals.\* These canals are described by Garman, one of the latest writers on the subject, as being supplied by the trigeminal. It may be mentioned that the minute branches for the cranial canal spring from the trunk of the nerve as it passes through the orbit and reach the surface by piercing the cartilage of the roof of the orbit at short and nearly regular intervals. A remarkable bundle of fibres runs obliquely across the upper border of the ophthalmicus superficialis at its origin, and reaching its anterior surface turns abruptly downwards to lie first in front of and afterwards under the buccal nerve. These fibres then form a plexus from which numerous twigs proceed to the conjoined roots of the hyomandibular and palatine nerves; they probably eventually reach and end in ampullæ and mucous canals.

5. *The Buccal Nerve.*—This nerve (5, fig. 1) springs by a large root from the side of the medulla, behind and on a slightly higher level than the root of the trigeminal. As the root passes outwards, it lies in the groove formed by the roots of the trigeminal and the posterior portion of the facial complex. After communicating freely with the ophthalmicus superficialis, it escapes with it through the cranial walls. Leaving the ophthalmicus superficialis, it comes into close contact with the outer surface of the Gasserian ganglion, and then lies between the maxillary and mandibular branches of the trigeminal. As the buccal nerve leaves the Gasserian ganglion, it presents a distinct swelling which is crowded with large bipolar cells. This may be called the buccal ganglion. The buccal nerve beyond the ganglion comes into intimate relation with the maxillary nerve, and as it runs forward under the contents of the orbit, it breaks up into branches which eventually reach the ampullæ and mucous canals of the snout not supplied by the ophthalmicus superficialis. The buccal nerve also sends branches to the anterior portion of the occipital mucous canal, and to the posterior part of the cranial mucous canal, and it sends a branch backwards which disappears under the hyomandibular cartilage. Further, by means of branches which run outwards, behind or under the contents of the orbit, the buccal nerve supplies the orbital and suborbital canals, apparently without any assistance from the maxillary and mandibular branches of the trigeminal.

*The Palatine and Hyomandibular Nerves.*—These nerves arise by a large root which lies between the trigeminal and auditory nerves, and partly under cover of the buccal nerve. This root is augmented by fibres from the plexus which, as mentioned above, is formed in connexion with the bundle of fibres that arches downwards from the ophthalmicus superficialis. Having received these additional fibres,

\* The names used for the mucous canals are those of Agassiz as modified by Garman.

the common root arches backwards, and enters a large foramen along with the auditory nerve. Leaving the auditory, it runs forwards through a canal in front of the auditory capsule. Having proceeded some distance (about 5 cm. in a large fish), it divides into two branches, a large branch (the hyomandibular) that proceeds outwards behind the spiracle, and a smaller branch (the palatine), which bends downwards towards the roof of the mouth. When the common trunk of these nerves is carefully studied, it is found to consist of two separate bundles, a small bundle which seems to be continuous with the palatine nerve, and a larger bundle which is continuous with the hyomandibular nerve. At the point of bifurcation there is a large collection of ganglionic cells, some of which lie in the palatine nerve and may be known as the palatine ganglion. Further, the two nerves are connected in front of the apparently compound ganglion by a number of fibres which have a somewhat plexiform arrangement.

6. *The Palatine Nerve.*—This nerve (6, fig. 1) at once gives off a number of branches (prespiracular) which are distributed to the tissues in front of the spiracle. The main trunk sends numerous branches to the roof of the mouth. Continuous with what may be known as the root of the palatine nerve, a distinct bundle of fibres runs outwards under the hyomandibular nerve (from which it receives one or more small branches), and passing over the hyomandibular cartilage, runs forwards to end in the fold of mucous membrane lying between the hyoidean and mandibular cartilages. I look upon this long slender nerve as corresponding to the chorda tympani of higher vertebrates.

7. *The Hyomandibular Nerve.*—This nerve (7, fig. 1) which increases immensely in size, beyond the ganglion, is chiefly concerned in supplying the large group of ampullæ that lies external to the spiracle, but it also supplies the mucous canals not already referred to, with the exception of the aural mucous canal and the canal of the lateral line. It further sends a branch backwards to muscles lying over and within the hyomandibular cartilage and the branchial apparatus.

In describing the facial complex, I have referred to a special ganglion on the ophthalmicus superficialis, to another on the buccal, and to a compound ganglion in connexion with the hyomandibular and palatine nerves. Gegenbaur considers the palatine nerve of Elasmobranchs as homologous with the great petrosal nerve of mammals. If this comparison holds, which I have every reason to believe it will, the interesting question arises—Is there any relation between the palatine ganglion of the Elasmobranch and the spheno-palatine ganglion of the mammal? And this leads to the further question—Are the ganglia of the ophthalmicus superficialis, buccal, and hyomandibular nerves related to the geniculate, otic, and submaxillary ganglia

of the higher vertebrates? These and other questions I shall hope to deal with in a future paper.

8. *The Trochlearis Nerve*.—This nerve (8, fig. 1) arises from the side of the brain immediately behind the optic lobe. It passes forward and upwards to pierce the cranium a considerable distance in front of the oculo-motor, it then dips downwards and outwards under the ophthalmicus superficialis to supply the superior oblique muscle. I have been unable to find any sensory branch passing from this nerve in *Lamargus*, and in no part of its length does it contain ganglionic cells.

9. *The Abducens*.—This nerve (9, fig. 1) has a striking resemblance to the anterior spinal nerves. It arises by three or four extremely slender rootlets which are in a line with the rootlets of the oculo-motor in front and the spinal nerves (ventral roots) behind. The rootlets unite to form a trunk which at first lies midway between the auditory and glossopharyngeal nerves. The trunk proceeds forward and perforates the cranial wall to reach and supply the external rectus muscle. The abducens nerve, like the oculo-motor and trochlearis, is devoid of ganglionic cells. It cannot be said to be specially related to the facial complex—to form as has been suggested its motor root.

10. *The Auditory Nerve*.—The auditory nerve (10, fig. 1) lies immediately behind and slightly ventral to the common root of the ventral portion of the facial complex. It runs outwards behind these nerves and enters the same cranial canal and at once divides into branches for the auditory apparatus. Although there is no distinct swelling, the root, some distance from its origin, is crowded with ganglionic cells.

11. *The Glossopharyngeal Nerve*.—This nerve (11, fig. 1) has been long considered one of the most primitive and typical of the cranial nerves. It arises from the side of the medulla in front of and in a line with the rootlets of the middle portion of the vagus, but under cover of the anterior portion of the vagus. The number of rootlets varies, but there is usually one large rootlet and two or three slender ones, and it receives a twig from one of the rootlets of the anterior portion of the vagus. The rootlets together form a small rounded nerve, which passes backwards and outwards through a special canal under the auditory capsule to reach and give two large branches (pre- and post-branchial) to the walls of the first true branchial cleft and a small branch (pharyngeal) to the pharynx. When midway through the walls of the cranium it presents a distinct swelling which is crowded with ganglionic cells. Immediately beyond the ganglion a small dorsal branch takes its origin, which passes upwards through the cranium to reach the skin over the auditory region. Apparently this dorsal branch does not assist in supplying either mucous canals or sensory tubés.

*The Vagus Complex.*—The vagus has been long held to represent a large number of nerves which, in most vertebrates, gradually coalesced as the branchial region became reduced in size or otherwise altered. Balfour states that the vagus arises in Elasmobranchs by four ganglionic roots, while more recently Beard and van Wijhe agree in describing the vagus as first appearing in the form of an unsegmented band which later blends with an epiblastic sensory thickening above the four posterior branchial clefts. The nerve for the second true branchial cleft is said, at an early period, to separate from this mass and develop a ganglion. Later the three posterior branchial nerves appear, but for these it is said there is usually only a single ganglion which, however, ventrally "shows a division into three portions." While the anterior portion of the vagus is described as supplying the second branchial cleft, the nerve to the lateral line is described as arising as a secondary formation from the epiblastic sensory thickening above mentioned. The lateral line nerve is usually described as springing from the common trunk, but Balfour, impressed with the importance of this nerve, says it "may very probably be a dorsal sensory branch of the vagus." That this surmise is practically correct will appear from what follows.

In *Lamargus* the vagus complex (12, fig. 1) arises by numerous rootlets disposed in three separate groups, an anterior group including two or three rootlets, a middle consisting of over twenty, and a posterior group of five or six rootlets. Hitherto the anterior portion of the vagus has been usually spoken of as Vagus I, or the nerve of the second branchial (first vagus) cleft. In *Lamargus* the anterior division of the vagus appears to be almost entirely concerned in supplying the mucous canal of the lateral line, and hence it may be known as the lateralis nerve, or nerve of the lateral line. Its right to be considered as a special nerve becomes all the more evident when it is mentioned that in some, if not all cases, it presents a ganglionic swelling. The lateralis nerve (l, fig. 1) seems in many respects comparable to the ophthalmicus superficialis of the facial complex, and like this latter nerve it springs from the side of the medulla on a higher level than the other divisions of the group to which it belongs. In several cases I have found it arising by one large root and a small accessory rootlet dorsal to and slightly in front of the roots of the glossopharyngeal. Having sent a twig from its small rootlet to the glossopharyngeal, it extends backwards to enter and traverse with the rest of the vagus the long cranial canal that runs backwards and outwards behind the auditory capsule. Soon after entering the canal it seems to blend with the rest of the vagus, but with care the whole or at least most of the fibres springing from above the glossopharyngeal can be shown to be directly continuous with the nerve of the lateral line. Soon after entering the canal it gives off a slender branch which,

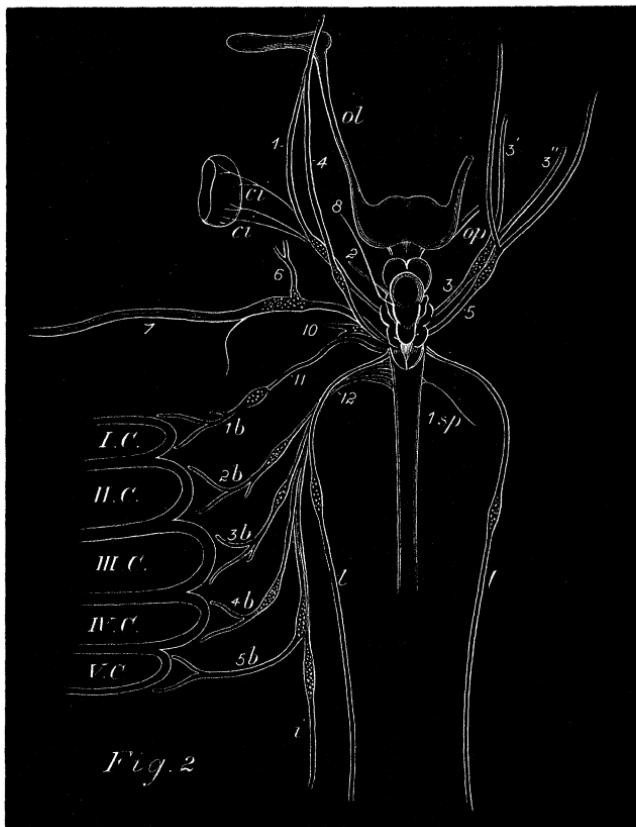
leaving the lateralis, arches upwards to supply the aural mucous canal and the anterior portion of the canal of the lateral line. Before escaping from the cranium the lateralis gives off another slender branch which is distributed to the succeeding portion of the lateral line. The rest of the lateral line is supplied by numerous slender fibres which spring from the lateralis as it passes backwards towards the tail.

In addition to the lateralis there are five other nerves in *Læmargus*, belonging to the vagus complex, viz., an intestinal and four branchial nerves. The first branchial nerve (the Vagus I of most authors), which is made up of the rootlets which lie immediately behind the root of the glossopharyngeal nerve, lies at first in close contact with the lateralis. This nerve (2b, fig. 1) presents a distinct ganglionic swelling as it passes through the vagus canal. Before escaping from the canal it breaks up into the three characteristic branches—post- and pre-branchial and pharyngeal. The three posterior branchials (3—5 b, fig. 1) and the intestinal (i, fig. 1) are derived from the common trunk. This trunk contains numerous ganglionic cells. In a large fish the compound ganglion (g, fig. 1) may reach a length of six or seven inches. Each of the branchials gives off the three usual branches, while the intestinal passes backwards towards the intestine and other structures. From the common trunk three or four slender filaments which extend outwards at a deeper level than the branches of the lateralis may represent dorsal branches of the posterior branchial nerves. It may be added that the vagus complex has no ventral roots; the so-called ventral roots of the vagus represent spinal nerves which have probably lost their posterior roots. In their distribution these nerves (1—2 sp., fig. 1) agree with spinal rather than with cranial nerves; two of them penetrate the occipital region of the skull on their way to the surface.

## II. *The Cranial Nerves of Raia batis.*

The cranial nerves of the skate, with the exception of those belonging to the vagus complex, closely resemble the corresponding nerves of *Læmargus*, hence, with the exception of the vagus, little more is necessary in the meantime than a short reference to their respective ganglia.

1. *The Ophthalmicus profundus.*—The root of this nerve (1, fig. 2), in *Raia* is more intimately connected with the root of the trigeminal than in *Læmargus*. The position and relations of the ganglion are of special interest. In *Læmargus* the ganglion of the ophthalmicus profundus was situated some distance behind, and it had no connexion with, the oculo-motor nerve. In *Raia* the ganglion of the ophthalmicus profundus lies some distance in front of the Gasserian ganglion, partly under cover of the rectus superior muscle and over the deep branch



of the oculo-motor. Further, the ciliary nerves, instead of springing from the trunk of the nerve some distance in front of the ganglion, as in *Læmargus*, usually spring from the under surface or outer margin of the ganglion, and hence the branches (ciliary) of the oculo-motor nerve, in passing to join the ciliary branches of the profundus, have to pass under the ganglion of the ophthalmicus profundus; the ganglion of the ophthalmicus profundus thus seems to be in a sense connected with the oculo-motor nerve, which doubtless explains why so many observers have described the ganglion of the ophthalmicus profundus as belonging to the oculo-motor. Were the root and trunk of the ophthalmicus reduced to slender filaments, the conditions found in some of the higher vertebrates would be arrived at, and the ganglion of the ophthalmicus profundus would appear to belong to the oculo-motor rather than to a branch of the trigeminal or an entirely separate nerve.

The oculo-motor, pathetic (2, 8, fig. 2), and abducens resemble the  
VOL. XLV.

corresponding nerves in *Læmargus*, and, as in *Læmargus*, they never present ganglia in any part of their course.

There is the usual ganglion on the trigeminal nerve, and this nerve (3, fig. 2), as in *Læmargus*, divides into maxillary (3', fig. 2) and mandibular (3'', fig. 2) branches, and sends a superficial ophthalmic branch to the snout along with the ophthalmicus superficialis of the facial. The facial complex, again, consists of four nerves, viz.:—(1) the ophthalmicus superficialis (4, fig. 2), with a large ganglion, which lies immediately above and in front of the Gasserian ganglion; (2) the buccal (5, fig. 2), with a ganglion lying over the origin of the mandibular branch of the trigeminal; (3) the palatine (6, fig. 2), (with an indistinct root containing ganglionic cells) which gives off palatine and prespiracular branches, and a branch which extends outwards to unite with fibres from the hyomandibular and bend round the hyomandibular cartilage, and eventually reach the floor of the mouth behind the mandible, thus resembling the chorda tympani; and (4) the hyomandibular nerve (7, fig. 2), which is chiefly distributed to mucous canals and the ampulla of sensory tubes. To the hyomandibular a large bundle of fibres is contributed, as in *Læmargus*, from the upper border of the ophthalmicus superficialis.

The auditory nerve (10, fig. 2) lies in contact with the hyomandibular, and has numerous ganglionic cells in its root.

The glossopharyngeal nerve (11, fig. 2) runs forwards from under the root of the lateralis nerve, and, bending backwards, passes outwards through a canal which opens into the floor of the cavity of the auditory capsule. Passing through the cavity of the capsule, the nerve next penetrates its outer wall, and at once expands to form a large oval ganglion, from which the usual branches take their origin. A dorsal branch, which reaches the surface of the head, does not seem to supply any portion of the occipital or aural mucous canals.

The vagus complex (12, fig. 2) in some respects seems to be more primitive in the skate than in any other Elasmobranch. It may be said to consist of six nerves, all of which can be readily distinguished, and each nerve presents a distinct ganglion. These nerves are (1) the lateralis (l, fig. 2), which springs by a special root above and in front of the glossopharyngeal nerve. The ganglion of the lateralis varies in position, being sometimes situated nearly two inches beyond the point at which the nerve issues from the cranium, in other cases only half an inch from its point of exit. A slender branch arising in the vagus canal arches upwards to supply the anterior portion of the canal of the lateral line, the aural, and part of the occipital mucous canals. The main trunk of the lateralis is distributed to the rest of the canal of the lateral line and to the posterior pleural canal. (2.) The four branchial nerves. The first three branchial nerves (2—4 b, fig. 2) acquire an independent existence almost as soon as the

vagus escapes from the cranium, while the fourth (*5 b*, fig. 2) is united with the intestinal nerve (*i*, fig. 2) until the level of the fifth branchial cleft is reached. In each of the three anterior branchial nerves the ganglion is situated within a short distance of the point of bifurcation into the post- and pre-branchial branches. The ganglion of the fourth nerve lies in contact with the common trunk from which it springs. (3.) The intestinal nerve (*i*, fig. 2) passes backwards, and has its ganglion immediately beyond the point where it separates from the last branchial. Sometimes one (*1 sp.*, fig. 2), or two ventral roots of spinal nerves arise under cover of the roots of the vagus and escape through the occipital region of the cranium, but as in *Læmargus* they never unite with any of the fibres of the vagus, and there is no reason for considering them as ventral roots of the vagus complex.

I am indebted to Mr. Sim, naturalist, Aberdeen, for the specimens of *Læmargus* required for the investigation.

The following list includes the more important papers and works referred to :—

- Balfour. ‘A Monograph of the Development of Elasmobranch Fishes.’  
 ‘Comparative Embryology.’
- Beard. “Sense Organs of Ichthyopsida,” ‘Quart. Journ. of Microsc. Science,’ 1885.  
 “The Ciliary and Motor-oculi Ganglion and the Ganglion of the Ophthalmicus profundus in Sharks,” ‘Anat. Anzeiger,’ 1887, Nr. 18—19.  
 “The Development of the Peripheral Nervous System of Vertebrates,” ‘Quart. Journ. Microsc. Science,’ October, 1888.
- Froriep. ‘Anat. Anzeiger,’ vol. 2, 1887.
- Garman. “On the Lateral Canal System of Selachia and Holocephala,” ‘Bulletin Mus. Comp. Zool., Cambridge, Mass.,’ vol. 17, No. 2.
- Gaskell. “On the Relation between the Structure, Function, and Distribution of the Cranial Nerves,” ‘Roy. Soc. Proc.,’ vol. 43.
- Gegenbaur. “Die Kopfnerven von Hexanchus,” ‘Jenaische Zeitschrift,’ vol. 6.  
 “Die Metamerie des Kopfes und die Wirbeltheorie des Kopfskeletes,” ‘Morphol. Jahrb.,’ vol. 13.
- Jackson and Clarke. “The Cranial Nerves of Echinorhinus spinosus,” ‘Journal of Anat.,’ vol. 10.
- Krause. “Ueber die Doppelnatur des Ganglion ciliare,” ‘Morphol. Jahrbuch,’ vol. 7.
- Marshall. “On the Cranial Nerves of *Scyllium*,” ‘Quart. Journ. Microsc. Science,’ 1881.  
 “The Segmental Value of the Cranial Nerves,” ‘Journal of Anatomy,’ vol. 16.
- Schwalbe. “Das Ganglion oculomotorii,” ‘Jenaische Zeitschrift,’ vol. 13.
- Stannius. ‘Das Peripherische Nervensystem der Fische,’ Rostock, 1849.
- van Wijhe. “Ueber d. Mesodermsegmente, and über die Entwicklung der Nerven des Selachier-Kopfes,” Amsterdam, 1882.

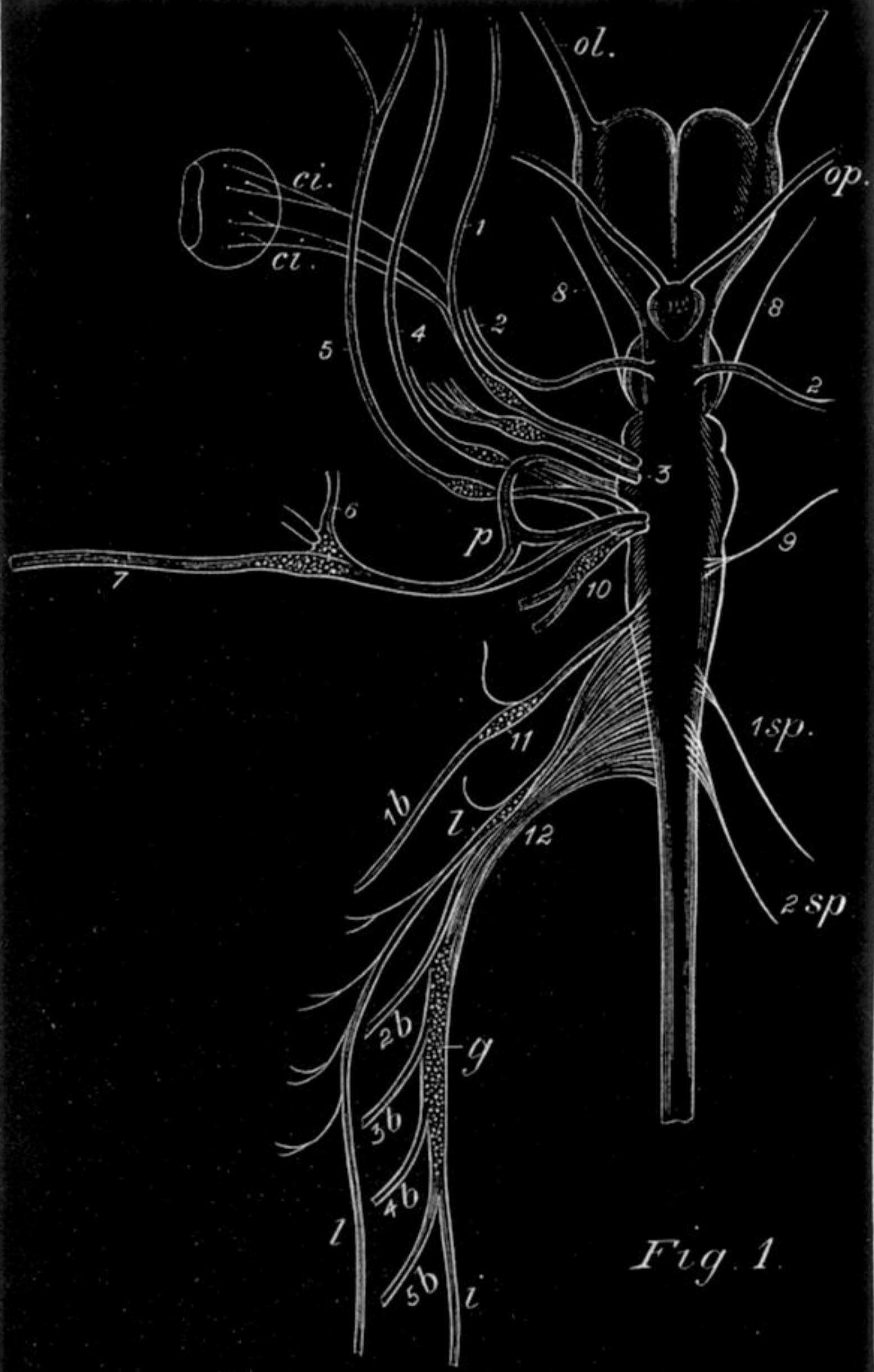


Fig. 1.

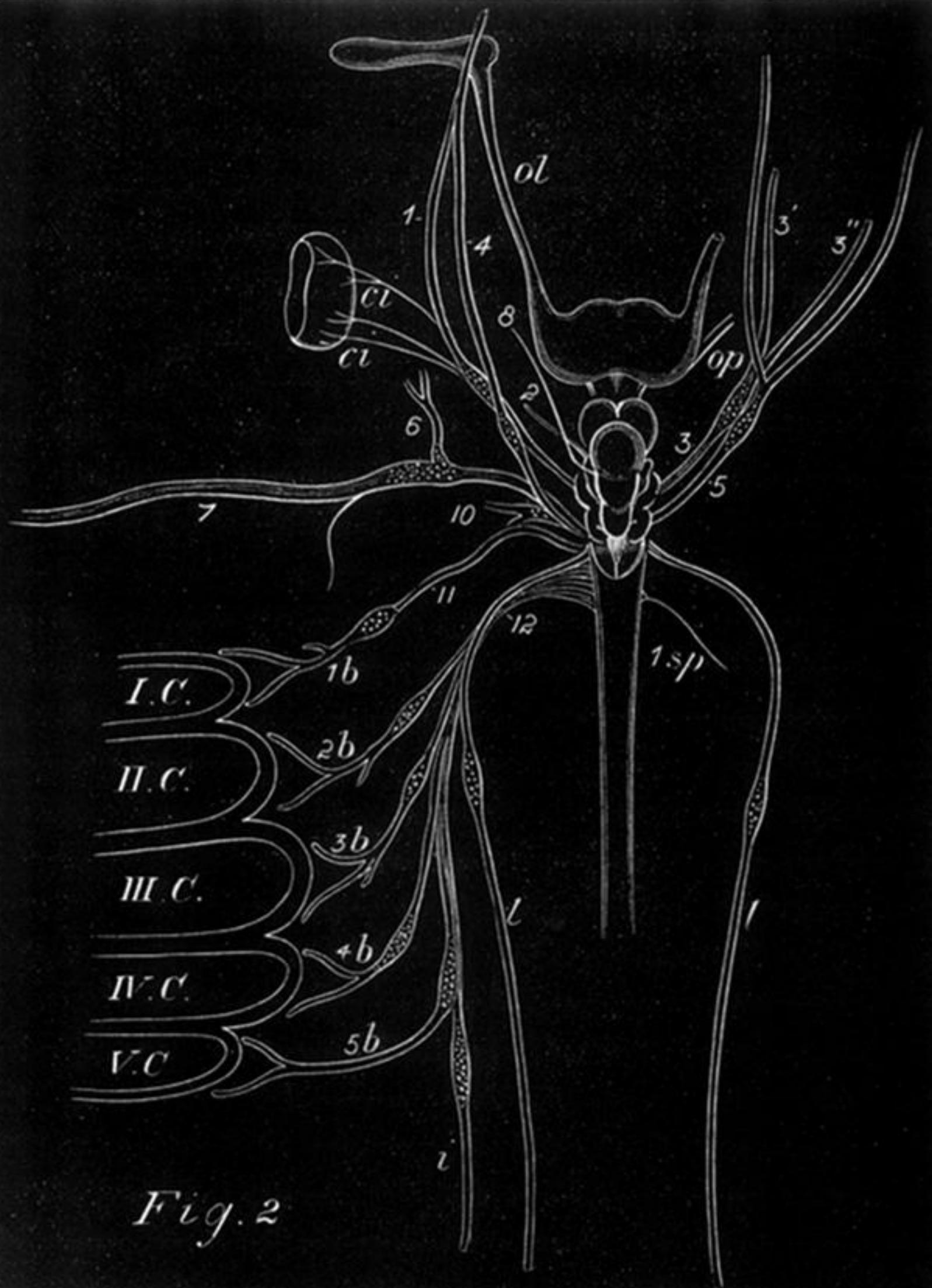


Fig. 2